First host record of *Argyresthia assimilis* Moriuti, 1977 (Lepidoptera: Yponomeutidae) and a description of its annual life history

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Abstract Seed predation by insects is an important factor influencing the evolution of synchronized annual fluctuations in the seed production of plant species. *Photinia glabra* (Rosaceae) is an evergreen bird-dispersed tree species that exhibits high variation in annual fruit production and heavy seed predation by insects. To identify the insect species infesting *P. glabra*, and to investigate seed predation patterns by these insects, we periodically sampled its infructescences from post-flowering until fruit ripening. We reared insects obtained from infested *P. glabra* fruits, and found that the insect species was *Argyresthia assimilis* Moriuti, 1977 (Lepidoptera: Yponomeutidae), whose host plant has been unknown since it was first described. Emerging females oviposited on *P. glabra* fruits in late September, usually laying a single egg per fruit. Larvae bored into the oviposited fruits and fed on seeds within the fruit. Final instar larvae exited the fruits to form cocoons in advance of fruit ripening in late December. Because *P. glabra* decreases the number of fruits after flowering (mid-May to mid-August), and because ripe fruits are heavily eaten by birds, immature life history of *A. assimilis* prevents egg loss by laying eggs after the decline in fruit number, and enables larvae to avoid bird predation within ripe fruits. This tight synchronization between insect and host plant life histories suggests that the host range of *A. assimilis* is restricted to *P. glabra* and its close relatives.

Key words Argyresthiidae, fruit and seed predator, *Photinia glabra*, Rosaceae.

Introduction

Seed predation by insects is considered an important factor influencing the evolution of masting or mast seeding, i.e., variable and synchronous seed production (Kelly and Sork 2002), in plant species. Masting strategies may allow plants to escape seed predation by alternately satiating and starving seed predators through variable seed production (the "predator satiation hypothesis", Janzen, 1971; Silvertown, 1980; Shibata et al., 2002). This hypothesis has been confirmed in some fagaceous species, which experience high seed predation pressure prior to dispersal (Shibata et al., 2002; Maeto and Ozaki, 2003; Kon et al., 2005). Although there have been few studies of this phenomenon in fleshy-fruited trees, berry production in rowan (Sorbus aucuparia L., Rosaceae) has been reported to be highly variable, with 2or 3-year cycles (Kobro et al., 2003). Satake et al. (2004) suggested that high variability in rowan berry production had evolved as a defense against its primary seed predator, Argyresthia conjugella Zeller (Yponomeutidae), called

Photinia glabra (Rosaceae) is an evergreen broadleaved subcanopy tree species native to the warm temperate regions of eastern and southern Asia, particularly in Japan, China, Myanmar, and Thailand (Ikeda et al., 2016). In Japan, this species is primarily distributed in Kinki and the eastern Shikoku and Chugoku regions, and disjunctively distributed in southwestern Kyushu (Hattori et al., 1987). P. glabra produces fleshy fruits on a dense corymbose cluster, and their fruits are heavily eaten by birds (Kuge and Hirayama, 2017). We observed that annual P. glabra fruit production is highly variable, with

[&]quot;the apple fruit moth" because the larva of this species feed on the apple, *Malus domestica* Borkh. (Rosaceae) (Okamoto, 1917; Ahlberg, 1927). However, female apple fruit moths lay eggs on apples only during intermasting years of rowan (Edland, 1978; Bengtsson *et al.* 2006), and larvae cannot complete their development on the apple (Ahlberg, 1927; Kobro *et al.*, 2003). Therefore, the apple fruit moth is now considered a specialist seed predator of rowan (Kobro *et al.*, 2003), implying that other *Argyresthia* species may also have narrow host ranges and tight relationships with their host plants.

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almost 2-year cycles observed in several forest stands in Kyoto, western Japan (Hirayama *et al.*, 2016). During poor crop years in this region, nearly all fruits suffer from insect damage (K. Hirayama, personal observation). Thus, insect predation could have a large impact on high annual fruit production variability in *P. glabra*, as reported in rowan.

The objective of this study was to identify the insect infesting *P. glabra* fruits in Kyoto, Japan and to investigate its seed predation patterns. We reared insects from infested fruits of *P. glabra*, and determined that the insect species was *Argyresthia assimilis* Moriuti (Lepidoptera: Yponomeutidae), which was originally described on the basis of a single male specimen (Moriuti, 1977). Thus, this is the first host plant record for *A. assimilis*; we also report the detailed immature life history and phenology of this species.

Materials and methods

Study site and species

We conducted periodic sampling of a P. glabra population in Takaragaike Hill in the northern part of urban Kyoto, western Japan (35° 3′ N, 135° 46′ E; 110-150 m a.s.l.). Takaragaike Hill includes a contiguously forested area of ca. 120 ha; it is primarily covered by a secondary deciduous broadleaved forest stand that was intensively coppiced until the 1960s (ca. 90 ha; Ministry of the Environment of Japan 2004-2014), and natural stands dominated by Pinus densiflora and artificial coniferous plantations (mainly Chamaecyparis obtusa). An evergreen broadleaved forest stand dominated by Castanopsis cuspidata has been rapidly expanding from the foot of the hill around a shrine and two temples (ca. 6) ha; Ministry of the Environment of Japan, 2004-2014). Detailed vegetation data were recorded by Hirayama et al. (2016).

P. glabra is one of main bird-dispersed tree species in the study site. Its flowers open in mid-May and its fruits ripen from late December to early January (K. Hirayama, personal observation). Most inflorescences are composed of more than 100 flowers, decreasing to approximately 50 by the fruit maturation stage (M. Sasaki, unpublished data). Mature *P. glabra* fruit are approximately 5-7 mm in width and 6-7 mm in length. The scientific name of the plant follows Ikeda *et al.* (2016).

Observation of insect damage in infested fruits

We collected two corymbose infructescences from each of five selected P. glabra trees at 2-week intervals after flowering (May 20) until fruit ripening (December 24) in 2016. During sampling, five immature fruits were randomly collected from each of the 10 collected infructescences; these were dissected to determine the type of insect damage. In mid-October, we began to find signs of larval boring (marks or holes) in fruits and seeds, and sometimes found larvae within fruits. Subsequently, we subjected another 7-10 fruits among each of the 10 infructescences to larva rearing after each sampling. In 2017, we also collected two infructescences from each of five selected trees (four of these trees were also used in 2016; one did not have a sufficient number of infructescences in 2017) at 2-week intervals after September 8, because this coincided with the peak adult emergence from the rearing samples collected in 2016. We conducted sampling until fruit ripening (December 18, 2017). In 2017, we dissected fruit to determine the type of insect damage in all immature fruits of one of the two infructescences from each of five sampled trees. We then subjected 10 fruits from the other infructescence of each sampled tree to larval rearing in late September, when we began to find eggs on fruits.

Larval rearing

Fruits, which were subjected to larval rearing, were set in a plastic Petri dish (9 cm diameter, 2 cm height) laid with a moistened wiping paper, with respect to each of sampled days and sampled infructescences. These plastic Petri dishes were maintained in the laboratory with less influence of air conditioning. Fruits collected in 2016 were checked once or twice per week until early October 2017, when adult emergence had ceased. Fruits collected in 2017 were checked once or twice per week until the end of March 2018. We took photographs of larvae, cocoons, and adults discovered in the rearing Petri dishes.

Three individual adults (two females, one male) that had emerged in mid-September 2017 from rearing samples collected in 2016 were used for egg collection. These adults were maintained with a fresh and intact *P. glabra* infructescence in a clear plastic case (25 cm width, 15 cm depth, 20 cm height) for 9 days, to observe the eggs and ovipositing sites of the insect.

Identification of emerged adult moths

We used four other male specimens that had emerged from the rearing sample collected in 2016 for species

Table 1. Descriptions of samples used in this study

DNA extraction and genitalia slide number	Sampling identification number	Sex	Sampling locality	Sampling date	Adult emergence date	Condition of specimen used	GenBank accession number
IO-338	P14	Male	Takara-gaike, Sakyo, Kyoto, Japan	Nov. 10, 2016	Sept. 11, 2017	Dried	LC421504
IO-339	P4	Male	Takara-gaike, Sakyo, Kyoto, Japan	Nov. 21, 2016	Aug.31, 2017	Dried	LC421505
IO-340	P6	Male	Takara-gaike, Sakyo, Kyoto, Japan	Nov. 21, 2016	Aug. 31, 2017	Dried	LC421506
IO-341	P1	Male	Takara-gaike, Sakyo, Kyoto, Japan	Nov. 21, 2016	Aug. 30, 2017	Dried	LC421507

identification. All specimens dissected in the present study (Table 1) were first targeted for DNA extraction. Total DNA was extracted from the abdomen of each specimen using a DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's protocol.

We amplified a barcoding region of the mitochondrial COI gene (658 bp) using the LCO1490 + HCO2198 primer set (Folmer *et al.*, 1994). Subsequent polymerase chain reaction (PCR), purification, and sequencing procedures were as described in Ohshima *et al.* (2018). Obtained sequences were aligned manually without ambiguity or indels using Mesquite software (Maddison and Maddison, 2016). Pairwise sequence distances were calculated by PAUP* software for Macintosh (ver. 4.0a159; Swofford, 2002) based on the Kimura's two-parameter (K2P) model. The obtained sequences were also analyzed using "identification tool" in the BOLD system software (ver. 3.0; Ratnasingham and Hebert, 2007) to search for similar sequences in the database.

Abdomens used for DNA extraction were placed in 10% KOH solution following the extraction procedure, and kept at 60°C for approximately 10 min to clean residual scales and internal soft organs. The abdominal segments and genitalia were then stained with aceto-fuchsin and mounted on a glass slide in Euparal. All specimens were deposited in the collection of the Entomology Laboratory at Kyoto Prefectural University, Kyoto, Japan. Adult wing patterns were examined using a Leica S6D stereoscopic microscope and genital morphology was observed using Leica M205C and DM2500 stereoscopic microscopes.

Results and Discussion

Species identification

Emerged adults showed wing patterns (Fig. 1) similar to those of *Argyresthia conjugella*, *A. assimilis*, and *A. mala*, according to Moriuti (1977), Yamauchi and Hirowatari (2013) and Liu *et al.* (2017). Observation of the male genitalia (Fig. 2) revealed that males have an extremely

long phallus (approximately 1.4 mm) (Fig. 2B) and a Y-shaped 8th sternite (Fig. 3), confirming that the moths that had emerged from *P. glabra* were *A. assimilis*.

However, there are at least four morphological differences between the original description in Moriuti (1977) and that of the present study. Moriuti (1977) reported that the socius is clothed with 22 scales, but the specimens examined in the present study have 20 (genitalia slide number, IO-341) and 21 (IO-340) scales. Exact scale numbers could not be obtained for the remaining two specimens, IO-338 and IO-339. Second is a number of spines on gnathos; the holotype described by Moriuti (1977) has five long spines on the gnathos, but the specimens examined in the present study have four (IO-338 and IO-339) or six spines (IO-340 and IO-341) (Fig. 2D, showing the case with six spines), though the spine number of the holotype falls between the numbers observed in the present study. Third is a character of cornuti of phallus. Although Moriuti (1977) noted that the cornuti of A. assimilis consists of a long spine and many spinules, the present specimens show rather inconspicuous cornuti (Figs. 2B, 4), each having a shorter spine (Fig. 4), and it seems that there is a variation was observed in the conspicuousness of cornuti. The last point is the adult body size. The specimens used in the present



Fig. 1. Emerged adult male of *Argyresthia assimilis* (DNA extraction and genital slide number IO-341). Scale bar: 3 mm.

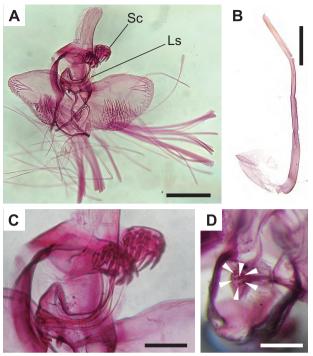


Fig. 2. Male genitalia of *Argyresthia assimilis* (DNA extraction and genital slide number IO-341). (A) Whole image except for phallus; (B) phallus; (C) enlarged socius and gnathos; (D) enlarged basal area of six long spines on gnathos (apical view). Triangular arrows indicate the positions of sockets on each long spine. Sc, socius; Ls, long spines on gnathos. Scale bar: 0.2 mm in A, 0.3 mm in B, and 0.1 mm in C and D.

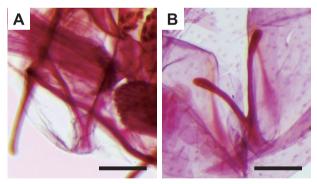


Fig. 3. Abdominal plate of male eighth sternite. (A) IO-338; (B) IO-339. Scale bar: 0.05 mm.

study showed larger wingspans than the holotype (9 mm), with a mean of 10.3 mm (n = 4, minimum = 10.0 mm, maximum = 10.6 mm).

Sequencing analysis of the barcoding region (658 bp) revealed that the maximum pairwise distance among the four examined specimens was 0.31% (2 bp), confirming that all four specimens belong to the same species.

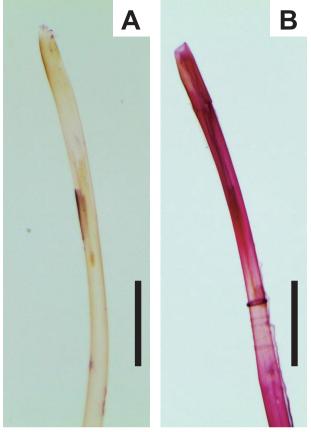


Fig. 4. Cornuti of phallus. (A) IO-338; (B) IO-339. Scale bar: 0.1 mm.

BOLD analysis showed that *A. conjugella* was the most closely related species within the database, with a minimum 3.26% pairwise sequence distance (21 bp).

The fact that Moriuti (1977) used only a single male specimen to describe A. assimilis, together with the sequence similarities observed among examined specimens in the present study, indicates that the recorded morphological differences represent intraspecific variation in A. assimilis. The wingspan depends on the angle of the spread forewings; therefore, we intended to compare the forewing lengths of our samples to that of the holotype, but we could not find the holotype of A. assimilis. In his paper, Moriuti (1977) stated that the A. assimilis holotype was stored in the collection of the Entomological Laboratory, University of Osaka Prefecture (OPU); however, the OPU staff informed the authors that the holotype is not currently in the collection (S. Kobayashi, pers. comm., 2018). Since no additional materials were collected from the type locality (Mt. Yoshinoyama, Nara, Honshu, Japan), neotype selection has been postponed

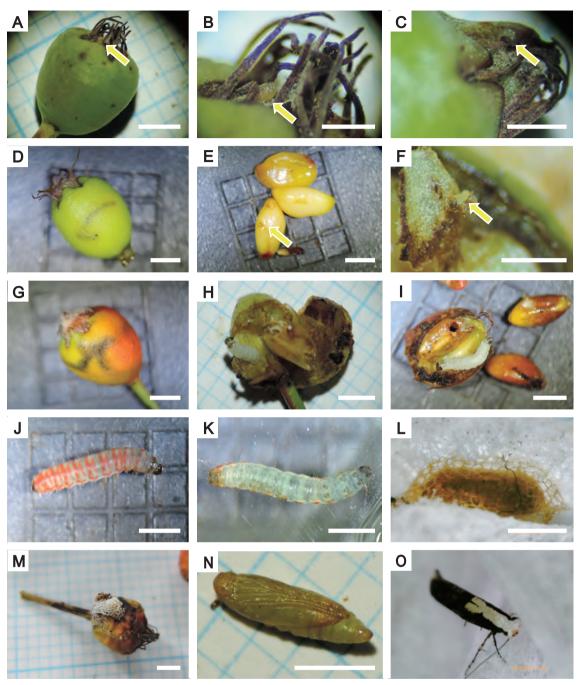


Fig. 5. Life history of Argyresthia assimilis. (A-C) Eggs of Argyresthia assimilis (tip of yellow arrow) laid on immature fruits of Photinia glabra. In most cases, a single egg is laid per fruit. (A) Egg laid on a pubescent carpel behind filaments of stamens; (B) enlarged photograph of the ovipositing site (same egg as shown in A); (C) egg laid in the gap between a sepal and a carpel. (D) Boring marks on oviposited fruit made by an early instar larva. (E) Hole made by an early instar in a seed within the oviposited fruit. (F) Early instar larva boring into seeds. (G) Boring marks on oviposited fruit by a later instar larva. (H, I) Feeding behavior of later instar larvae and predated fruits. Large holes are made in seeds and frass presents within fruits. (J, K) Final instar larvae. (J) Dorsal view; (K) ventral view. (L) Cocoon formed on the surface of wiping paper in a plastic Petri dish. (M) Cocoon settled on a fruit where a larva had bored. (N) Pupa exposed from a cocoon. (O) Resting posture of an emerged adult. Scale bar: 1 mm in B, C, and F, and 2 mm in others.

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until enough specimens can be collected from the type locality.

Life history of A. assimilis

In the laboratory, A. assimilis adults emerged from late August until early October, with a peak in early September 2017 from rearing larvae collected in 2016. Based on the observation of periodically sampled P. glabra fruits in 2017, we began to find eggs on the fruits from late September (Fig. 5A-C). Because rearing females began to oviposit within 5 days in the laboratory, adults in the wild are expected to emerge from mid-September. This is consistent with that of Moriuti (1977); the male specimen used for the species description was collected on September 28, 1968. Other collection records of A. assimilis adults from central Honshu Island are also compatible with the adult emergence dates of the present study (October 7 and 14, 1994 in Osaka; Koshino and Unesaki, 1995). Koshino and Unesaki (1995) also reported that three adults (one female and two males) were collected on April 23, 1994 in Osaka. However, this sampling date was mistyped; the correct collection date was September 23, 1994, as confirmed by the OPU staff (S. Kobayashi) through label verification; thus, all collection records of adult A. assimilis in Koshino and Unesaki (1995) are consistent with the observations of the present study.

A. assimilis has also been recorded from the northernmost main island, Hokkaido, where *P. glabra* is not distributed. Adults were collected earlier in Hokkaido than in central

Honshu (August 12, 1988 [Ijima, 1993] and July 26, 1994 [Kawahara, 1999]). One possible reason for this earlier emergence is that *A. assimilis* is associated with different host plants in these localities. Another possibility is misidentification due to the similarity of its wing pattern with those of closely related species. Indeed, Ma and Sun (1982) misidentified *A. mala*, which is distributed in China, as *A. assimilis* and reported it as an apple pest. Ma and Sun (1982) found that *A. mala* adults emerged from June until July, and that this phenological pattern was somewhat similar to the two abovementioned collection records from Hokkaido. Thus, future studies should examine the hypothesis that *A. mala* and other closely related species are distributed in Hokkaido.

The number of P. glabra fruits per infructescence decreased soon after flowering until mid-August, then remained stable until ripening (M. Sasaki, unpublished data; Fig. 6). This decrease in the number of fruits until mid-August should be mainly ascribed to intrinsic factors of the plants, such as flower and ovary abortion (Jordano, 1989; Traveset, 1994). A. assimilis oviposition occurred after P. glabra fruit numbers had declined; the size was 4.28 ± 0.10 mm in width and 5.96 ± 0.17 mm in length (mean \pm SE, N = 9). Ovipositing females typically laid a single egg per fruit (more than 80% of cases), usually on a pubescent carpel behind stamen filaments (Fig. 5A, B) but sometimes in the gaps between sepals and carpels (Fig. 5C). This oviposition habit is similar to that of a closely related species, A. conjugella, whose females lay only a single egg at the apex of each rowan berry, between

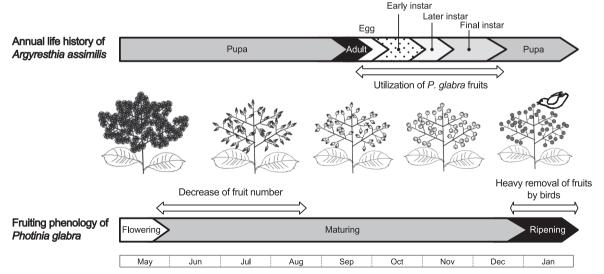


Fig. 6. Schema of the relationship between the annual life history of *Argyresthia assimilis* and fruiting phenology of *Photinia glabra*.

or close to the remains of the stamen (Jaastad et al., 2005).

We began to find boring marks on fruit surfaces (Fig. 5D) and holes in seeds within fruits (Fig. 5E) from early October in both 2016 and 2017. We found early instar larvae with white bodies and brown heads after early October among the dissected fruits (Fig. 5F). We began to find later instar larvae (Fig. 5G-I) from late October. Final instar larvae (Fig. 5J, K), which had red dorsal stripes on greenish bodies and were 5-7 mm long, were found from early November in both 2016 and 2017, with a peak in late November 2016 and early December 2017. We typically found one larva per dissected fruit (in more than 90% of cases) in both years. The final instar larvae that we reared usually exited the fruits to form cocoons from mid-November until mid-January, with a peak at the end of November 2016 and early December 2017. The cocoon usually settled on the surface of the wiping paper in the plastic Petri dish (Fig. 5L), and was sometimes found on fruits where the larva had bored (Fig. 5M). In dissected cocoons, we observed pupae that were approximately 4 mm long (Fig. 5N). *P. glabra* fruits ripen from late December until early January at the study site (K. Hirayama, personal observation). Therefore, most A. assimilis larvae would leave P. glabra fruits to pupate before fruit maturation; mature fruits were likely eaten by birds in a high probability (Kuge and Hirayama, 2017).

Fig. 6 shows a schema of relationships between the annual life history of A. assimilis and the fruiting phenology of P. glabra. In the closely related A. conjugella, females oviposit on small rowan berries shortly after the petals fall in June in Norway, and larvae bore into fruits immediately after hatching (Kobro et al., 2003). A. conjugella larvae complete their development within the berries by mid-August, and leave fruits for pupation and hibernation in litter on the ground (Kobro et al., 2003). Although Kobro et al. (2003) and the present study were conducted in different locations, with an approximately 25° difference in latitude, patterns of fruit use by larvae were similar between the species, in terms of synchronization between fruit ripening and insect development. In conclusion, A. assimilis prevents egg loss by laying eggs following a seasonal decline in fruit number, and enables larvae to avoid bird predation by leaving fruits before ripening (Fig. 4). Such tight synchrony with the host plant suggests that A. assimilis is a specialist seed predator of P. glabra in the study area.

Future studies on A. assimilis oviposition rates and P. glabra fruit production spanning multiple sequential years would contribute to uncovering the mechanisms underlying high annual variability in P. glabra fruit production, as reported in rowan. The fact that P. glabra fruits were heavily infested with A. assimilis larvae in the present study provides an opportunity to describe the morphology of the larvae, pupae, and female genitalia of this species in detail in future studies.

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摘 要

セジロメムシガ (スガ科) の寄主初記録と生活史 (平山貴美子・佐々木瑞季・大島一正)

本種は、Moriuti (1977) によって、奈良県吉野山産のオス 1個体の成虫標本をもとに記載され、その後数例の採集記 録はあったが寄主植物は不明のままであった。著者らが研 究をおこなっている京都市近郊二次林において、主要な鳥 散布型の常緑広葉樹であり、果実生産に大きな年変動のみ られるカナメモチについて、凶作年には殆どの果実におい て昆虫による加害がみられるため、季節的な果実の加害状 況の調査と加害昆虫の飼育をおこなった. その結果, この カナメモチの加害昆虫はスガ科のセジロメムシガであるこ とが明らかとなった。カナメモチは集散花序であり、5月 中旬に開花後、8月中旬にかけて花序内の果実は数多く落 下し、約半分に減少していく. 野外におけるセジロメムシ ガの雌成虫による産卵は、この花序内果実数の減少がほぼ 収束する9月後半よりみられ、1果実あたりの産卵数はお およそ1卵となっていた. 孵化した幼虫は速やかに果実や 果実内の種子に穿孔し、内部を摂食していた、終齢幼虫の 多くは、果実が成熟する12月後半より前に果実から脱出 し、繭を形成していた.カナメモチは果実成熟後、高い確 率で鳥に被食される. セジロメムシガの卵・幼虫段階にお ける生活史は、カナメモチの果実に強く依存し、さらにカ ナメモチの果実成熟初期における果実数の減少や、果実成 熟後の鳥の被食による個体数の減少をも免れていると考え られた. このようなカナメモチ果実とセジロメムシガの生 活史の同調は、セジロメムシガがカナメモチとその近縁種 の果実食スペシャリストであることを示唆している.

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